

Long-term anthropogenic shaping of global species distributions

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Anthropogenic shaping of global biodiversity is undisputedly one of the major impacts of humans on Earth's ecosystems. As our planet experiences its sixth 'mass extinction event' (Barnosky et al. 2011), the effect of human-mediated landscape modification, habitat fragmentation, overexploitation and species invasions could not be more apparent (refs). These transformations are linked largely to the industrial economies, dense transport networks and burgeoning populations of contemporary human societies. Accordingly, human alteration of species distributions has been characterised as a modern phenomenon with limited, and largely insignificant, historical antecedents. This conventional understanding is erroneous and fails to take into account several decades of archaeological, palaeoecological and genetic research that are beginning to reveal a long and underappreciated history of human transformation of global biodiversity.

Here, by drawing upon findings from a range of new methods and datasets, including new cross-disciplinary research programmes, we reveal a pattern of significant long-term, anthropogenic shaping of species distributions on all of the earth's major occupied continents and islands. Even prior to the Age of Discovery, cumulative human activities over millennia had resulted in dramatic changes to the abundance and geographic range of a diverse array of organisms across taxonomic groups. Exceedingly few, if any, regions could be characterised as pristine. Extinction has been the starkest of these anthropogenic impacts, but changes to species abundance, composition, community structure and richness have also increasingly been demonstrable.

In this analysis, we examine four key phases of anthropogenic change: the late Pleistocene near global dispersal of *Homo sapiens*; the emergence and spread of agriculture beginning in the early Holocene; the colonisation of the world's islands; and the pre-modern expansion of urbanisation and trade beginning in the Bronze Age. Our review is not exhaustive, but rather highlights key trends, including the significant prehistoric and historic reorganisation of species distributions at local, regional and intercontinental scales; a broadly accelerating but uneven rate of alien species introductions across a multitude of geographical regions; and the involvement of a wide range of species, including plant and animal domesticates, as well as a diverse array of wild, commensal, invasive and pathogenic species. We address the implications of these anthropogenic changes to species abundance, diversity and distribution for how we study and conserve the earth's biomes.

Four key phases of anthropogenic transformation

Global colonisation

Homo sapiens evolved in Africa approximately 160-200 kya (refs), and by 12 kya had dispersed to the far corners Eurasia, Australia, and the Americas. Human populations were adapted to a broad range of terrestrial and maritime environments, dwelling in savannahs, alluvial plains, tropical forests and coastal and island environments (Boivin et al. 2013; O'Connor et al. 2011; Roberts et al. 2015). Studies suggest that the period of global human expansion, particularly after 50 kya, was one of increasing technological sophistication (Shea & Sisk 2010; Shea ref; O'Connor et al. 2011; Balme 2013) and demographic increase (e.g., Atkinson et al. 2007; Powell et al. 2009; Mellars & French 2011).

The same time period also saw dramatic changes to a class of animals, larger than 44 kg, known as megafauna. Between 50 and 10 kya, at least 101 of 150 genera of Earth's megafauna went extinct (Barnosky 2008). Anthropogenic causes have long been invoked (Martin; Sandom et al. 2014), though not without controversy. Recent studies often acknowledge the potential for synergistic effects, particularly between human and climatic agents (e.g., Barnosky & Lindsey 2010; Nogués-Bravo et al. 2010; Munzell et al. 2011; Prescott et al. 2012). They also note the potential for variability in the relative importance of different causal factors across regions and species (Barnosky et al. 2004; Lorenzen et al). Australian megafaunal extinctions, for example, do seem to be best explained by the arrival of humans (Barnosky, etc). Recent high resolution data from Australia shows that megafaunal collapse occurred during a period of climatic stability and can be most closely correlated with human arrival (Rule et al. 2012). Climatic factors are also seen as insufficient to explain South American extinctions (Nogués-Bravo et al. 2010).

Implicating humans in late Pleistocene megafaunal extinctions infers an anthropogenic role in some of the major biosphere transformations that followed on from the demise of large-bodied animals (Barnosky 2008; Johnson 2009; Gill 2013). Studies suggest that megafauna were often keystone species (Gill 2013) whose disappearance had dramatic effects on ecosystem structure (Gill et al. 2009; Rule et al. 2012), fire regimes (Gill et al. 2009), seed dispersal (Janzen & Martin 1982), land surface albedo (Doughty et al. 2010) and nutrient availability (Doughty et al. 2013). New multiproxy paleoecological datasets from North American and Australian lake deposits demonstrate that significant vegetation change followed Late Quaternary megafauna extinction, with implications for fire regimes (Gill et al. 2009; Rule et al. 2012; Lopes dos Santos et al. 2013). Modification of land surface albedo may have contributed to climatic warming (Doughty et al. 2010). Recent work suggests that Pleistocene megafaunal extinctions resulted in large and ongoing disruptions to terrestrial biogeochemical cycling at continental scales (Doughty et al. 2013).

There are other lines of evidence suggesting that humans began to more intensively shape the other species around them in the Late Pleistocene. In Highland New Guinea, several lines of evidence, most notably increased burning,

have been linked to deliberate clearance of forest patches to promote the growth of useful plants (Hope 2009; Summerhayes et al 2010). Anthropogenic burning of the landscape has also been suggested for other parts of the world, including Australia and the Americas (Pinter et al. 2011; Australia ref; though see Mooney et al. 2011). There is evidence to suggest that human plant use intensified in the Late Pleistocene in various regions of the world (e.g., Piperno et al 2004; Liu et al. 2013). The use of a wider range of resources, seen in both floral and faunal datasets in various locations, might reflect increased sedentism and control of particular territories (Zeder). Intensification in some cases led to species depletions (refs). For example, impacts to the species composition and genetic diversity of limpets in northwestern Spain are indicated by one recent study (Turrero et al 2011).

The human-mediated translocation of species also dates back to the Late Pleistocene. Anthropogenic translocations are most visible in island contexts, where transport by non-aquatic species would have necessitated human agency. Islands were also frequently depauperate (refs) and the deliberate translocation of certain species was probably effected to increase their habitability. For example, the cuscus *Phalanger orientalis*, endemic to New Guinea, was transported throughout eastern Indonesia, the Solomon Islands and the Bismarck Archipelago beginning in the terminal Pleistocene, becoming a key subsistence species (Flannery & White 1991; Latinis 1996; Heinsohn 2003). The faunal assemblage at the site of Matenbek in New Ireland was dominated by *P. orientalis* from 18 to 20 kya (Gosden 1995; Allen in press). Several other New Guinea marsupials appear to have been exported to surrounding islands in the terminal Pleistocene (Heinsohn 2003).

Mounting evidence indicates that the continental dispersals and global increase in human biomass of the late Pleistocene were linked, albeit in complex ways, with a variety of species extinctions, extirpations, and translocations, and new modes of niche modification. While assessment of anthropogenic impacts in the Pleistocene remains challenging, new approaches offer potential solutions to long-standing problems posed by limitations of preservation and chronological resolution.

Emergence and spread of agriculture and pastoralism

The beginning of the Holocene epoch (<11.7 ky) marked a fundamental shift not only in climatic and geological regimes globally, but also human societies. With the earth recording its warmest atmospheric temperatures in over 100 ky and entering a period of unprecedented climatic stability (Richerson et al. 2001), the epoch saw the emergence and spread of what is almost certainly the most important development in human history: agriculture. The Neolithic, as this transition is known, opened the way for a radical transformation in the human capacity for niche construction. The keeping and managing of animals, and the cultivation of plants led to new evolutionary pressures on a growing range of species, and the emergence of novel domesticated forms. The production of food also enabled radical expansions in human population sizes (Bocquet-Appel 2011).

One of the major outcomes of the Neolithic was the spread of agriculture from relatively few centres of domestication to, eventually, large swathes of both the Old and New Worlds. This had unprecedented and enduring impacts on species distributions. On the one hand, it resulted in massive increases in the distribution of a range of human-favoured species, including not only crops and herd animals, but also a range of weeds, commensal species and pathogens. On the other hand, and as a direct result of these expansions, it resulted in the contraction and fragmentation of populations of a broad range of other species.

Some of the earliest plants and animals to become the focus of human management were those in the Levant, including the wild grasses that would become domesticated wheat and barley, and the goat, sheep and cattle that would be rendered smaller and docile by human breeding. These were domesticated by x. Much of this agricultural package subsequently spread across Europe during the Neolithic. Archaeobotany records the spread of wheat as far as westernmost Europe by 8000 BP. Today, wheat is grown on more land area than any other cultivated crop (Curtis, FAO website), across some 218 million hectares of land, the vast majority outside its area of origin, in distant parts of eastern and southern Asia and the New World. Sheep, goat and cattle also spread, northwestwards to Europe, reaching x by y, but also east and south

Similar journeys are suggested for other crops and domesticates. Few sentences on spread of corn in New World and rice in Asia. Genetic evidence suggests that dog domestication was initiated around the time of the Last Glacial Maximum (Thalmann et al. 2013). The human shaping of this species from wolves, and promotion over other carnivores from the terminal Pleistocene onwards, would eventually see dogs adapt to the human niche (Axelsson et al. 2013) and become the world's most abundant and ubiquitous carnivore, with an estimated 700 million-1 billion dogs worldwide today (Ritchie et al. 2014).

Also spreading during the Neolithic were a variety of weed species, invasive species and pathogens. In Europe, some crop weeds derived ultimately from the Near East, while others were European plants promoted by anthropogenic disturbance and the novel ecologies of cultivated plots (Colledge et al. 2005; Coward et al. 2008). Another sentence on promotion of weed plants elsewhere – Asia? The Neolithic northwest European elm decline (give dates) may have been caused in part by the spread of a pathogen, such as the fungal disease *Ophiostoma*, carried by the elm bark beetle *Scolytus scolytus* (Clark & Edwards 2004; Lamb & Thompson 2005; Waller 2013). Zoonotic diseases, passed from animals to humans, also spread as part of Neolithic population expansions.

The spread of human populations and the species they favoured altered existing species, sometimes in synergy with Holocene climatic changes. Neolithic cultivation and husbandry generally demanded a more open landscape, facilitated through various means from fire to the cutting and coppicing of trees (Tinner et al. 2005; Yerkes et al. 2012; Innes et al. 2013). Numerous studies demonstrate that the early Neolithic corresponded with shifts away from deciduous tree cover in various regions of northern Europe (Poska et al. 2004),

for example. Forest removal and agricultural activities also impacted lake biota, including lacustrine microfloras and microfaunas (diatoms, macrophytes, foraminifera, etc.). Palaeolimnological studies at various lake sites in lowland Europe suggest human-mediated increases in mesotrophic-eutrophic planktonic diatoms, including *Asterionella formosa* and *Fragilaria crotonensis*, by 5000 BP (Wilkinson et al. 2014). Land cover changes appear to have been linked to increasing human populations in the Neolithic (Lechterbeck et al. 2014; Woodbridge et al. 2014). The European evidence also supports periods of forest resurgence (O'Connell et al. 2014), linked to demographic collapse (Stevens & Fuller 2012; Shennan et al. 2013; Timpson et al. 2014; Whitehouse et al. 2014).

A short paragraph on Neolithic land cover change evidence from Near East plus a few other parts of the world that have data – China? New World? New Guinea?

Recent research is demonstrating the role of early pastoral economies in reshaping species distributions in Tibet, Mongolia, the eastern Hindukush, Nepal, and Central Asia (e.g., Miehe et al 2007, 2014; Kaiser et al. 2009a; Spengler 2014). For example, multiproxy palaeoecological evidence suggests that as in other nearby regions, the landscapes of the eastern Tibetan highlands are largely anthropogenic, created by pastoralists who transformed forests and tall grassland into 'golf course-like' pastures beginning 7-8 kya BP (Miehe et al. 2008, 2014; Schlütz & Lehmkuhl 2009). Grazing of sheep and goat from the Near East as well as locally-domesticated yak massively increased herbivore load, and together with forest burning, significantly accentuated climate-induced vegetation changes, creating a largely cultural landscape in eastern Tibet. Resultant changes in albedo may have impacted the monsoon system (Schlütz & Lehmkuhl 2009).

Island colonisation

The capacity of island contexts to intensify both human impacts and their archaeological visibility marks them out for special consideration here. The colonisation of the world's oceanic islands accelerated significantly in the Holocene (and particularly Middle and Late Holocene), in association with the spread of agricultural and semi-agricultural societies and the development of maritime technology (Anderson 2010; Rick et al 2014). Island colonists frequently carried with them a 'transported landscape' (Kirch 1997, 2000) of domesticated animals, commensals, crops, weeds and other species. Many of the flora and fauna that humans brought with them helped create new anthropogenic ecosystems that enabled islands to more adequately support human populations.

The high endemism, naïve and/or disharmonic fauna, and low functional redundancy of many island ecologies (Saddler 1989; Courchamp et al. 2003) also, however, resulted in heightened susceptibility to ecological transformation by these transported species, and the modification of island environments through anthropogenic fire, deforestation and predation. In some parts of the world, waves of extinction followed island colonisation (Diamond 1989; Burney 1997; Saddler 1999). Ninety-five percent of bird and terrestrial mammal

extinctions since 1500 have been on islands, highlighting the particular susceptibility of islands to anthropogenic biotic change (Loehle & Eschenbach 2012). A range of other species from land snails to plants and marine animals have been similarly impacted, though island diversity conveys significant regional and sub-regional variability (Saddler 1999). Anthropogenic impacts to island species are particularly visible to archaeologists because they are for the most part relatively recent (<10 ka) and occurred in pristine environments during a period of relative global climatic stability (the Holocene). Anthropogenic translocations are also particularly apparent on islands since many species are unable to travel across the sea without human assistance. This makes islands optimal 'model systems' (Vitousek 2002) for study the prehistoric reshaping of species distributions by humans.

While islands worldwide saw major ecological transformations following human colonisation, some of the best-studied examples come from the Pacific. There has been debate about the relative impacts of natural and anthropogenic processes in the region (e.g., Burney 1997; Nunn, Spriggs 1997, Hunt, etc), and both have undoubtedly played a role, but a now significant body of evidence supports significant ecological transformations by early Polynesians (Spriggs 2010). Bearing minimal technology, but with advanced maritime capabilities, Polynesian peoples began to move across the Pacific by 3500 ya (Kirch 1997), colonising previously uninhabited islands and bringing with them a 'portmanteau biota' (Crosby 1986) consisting of both domesticated plants (e.g., taro (*Colocasia esculenta*), yams (*Dioscorea* spp.), sweet potato (*Ipomoea batatas*) and banana (*Eumusa* spp.)) and animals (including pig (*Sus scrofa*), chicken (*Gallus gallus*) and dog (*Canis familiaris*)), and synanthropic species like the Pacific rat (*Rattus exulans*) (Anderson 2009). The domesticates carried by Polynesians were undoubtedly critical to their ability to survive and indeed flourish on the islands of the Pacific, which often lacked edible plants and possessed limited nonmarine fauna beyond birds, fruit bats, and sometimes lizards (Spriggs 1997). Nonetheless, together with hunting activities, burning practices and cultivation regimes, these introduced species also massively impacted native plants and animals, radically shaping biodiversity and disrupting ecosystems.

Some of the clearest evidence for Polynesian impacts comes from bird fossils. These demonstrate the extinction of thousands of bird populations in the Pacific following Polynesian colonisation. Steadman (1995) suggested that 60 species of endemic land bird went extinct in the Hawaiian Islands alone. A more recent estimate puts the number at 70-90, and observes that given the demonstrated limitations of the fossil record, this is probably an underestimate by at least half (Pimm et al. 2006). A recent modelling-based study, using a Bayesian mark-recapture approach to model gaps in the fossil record and quantify losses of nonpasserine landbirds on 41 Pacific islands, found that two-thirds of the populations on these islands went extinct in the period between first human arrival and European contact (Duncan et al. 2013). The disappearance of bird species impacts important ecosystem processes like decomposition, pollination and seed dispersal, leading to trophic cascades (Şekercioğlu et al. 2004; Anderson et al. 2011). Extinctions often occurred rapidly (Martin & Steadman

1999; Steadman et al. 2002; Anderson 2009), and included not just birds, but also various species of bat, landsnail, and lizard (need refs; Steadman et al. 2002). While floral extinctions have not been as well-studied, it is clear that a range of plant species also went extinct, most notably in the palm family, *Arecaceae* (Prebble & Dowe 2008). Pollen and wood charcoal analysis demonstrate at least 18 plant extinctions on Rapanui (Easter Island), and show dense palm forest disappearing within 200 years of human settlement (Hunt 2007; Prebble & Dowe 2008).

New Zealand's fossil and archaeological records document a vast number of vertebrate extinctions in the aftermath of Polynesian arrival 750 years ago (refs). Data from new higher resolution studies is demonstrating that these transformations were even faster and more significant than previously recognised. High-precision chronological data (Perry et al. 2014) indicate that moas, which had been thriving and genetically stable prior to colonisation (Allentoft et al 2014), were exterminated within two centuries of human colonisation. Recent studies of ancient DNA also suggest that several New Zealand species thought to have survived these early human impacts were actually driven to local extinction. An endemic sea lion lineage (*Phocartos* spp.) and an endemic penguin (*Megadyptes* spp.) were both eliminated soon after human arrival and then replaced within a few centuries by a genetically divergent clade from the remote subantarctic region (Boessenkool et al. 2009; Collins et al. 2014).

Polynesian arrival significantly transformed landscapes on many Pacific islands, altering plant species composition and abundance (recent refs). A recent palynological study suggests that Polynesians modified Tonga landscapes through the burning and clearing of indigenous rainforests, and the introduction of at least 40 plant species, mostly trees, shrubs and herbaceous cultigens (Fall 2010). Polynesian activities also altered the abundance and distribution of useful indigenous plant species on Tonga, favouring, for example, such tree species as *Canarium harveyi*, *Casuarina equisetifolia*, *Erythrina variegata* and *Pandanus tectorius* (Fall 2010). A wide variety of plants were also brought to the subtropical islands of Polynesia in the pre-European era, including at least 17 unintentionally introduced weed species (Prebble 2008). Human-mediated fire regimes significantly altered vegetation distributions across the Pacific (Spriggs 2010; other refs), and the impacts were often rapidly felt. New AMS dating evidence from New Zealand suggests that dramatic forest loss and conversion of nearly half of native forests to open vegetation, resulting from anthropogenic fires, occurred within decades rather than centuries of the initial arrival of a small founding population (McWethy et al. 2014).

A growing dataset also supports significant human transformation of Mediterranean island landscapes beginning soon after human colonisation. Despite suggestions of a Palaeolithic presence on certain islands (refs), maritime colonisation in this region appears to have been largely a Holocene phenomenon (ref), associated with the spread of early farmers into the region. Cyprus, for example, was colonised by farmers from the Near East by 10.6 kya (Vigne et al. 2012). Like other islands in the region, it had a highly endemic and impoverished

faunal population that was replaced by mainland species shortly after colonisation (Vigne et al. 2012). There is insufficient evidence at this time to resolve debates about the role of humans in the extirpation of Cyprus endemics, but the anthropogenic nature of the species introductions to the island is undisputed. Early colonists imported domestic cereals, pulses, sheep, goat, cattle, pigs, small domestic dogs and cats, as well as mainland game animals like fallow deer and fox (Zeder 2008; Vigne et al. 2012). Commensal mice were present by 10.4 ka (Vigne et al. 2012). The introduction of managed wild boar that were hunted by humans appears to have occurred as early as 11.4-11.7 ka (Vigne et al. 2009), prior to Neolithic habitation. The introduction of diverse faunal species dramatically reshaped the biota of Cyprus and enabled early settlers to adapt to an environment with a low density of food animals (Vigne et al. 2012).

The long-term anthropogenic shaping of Mediterranean island landscapes is clear from a broad range of studies. Discuss other Mediterranean islands re. Neolithic introductions and environmental impacts, landscape alteration.

Caribbean – Rick et al 2014

A broad range of studies support similar trends worldwide. Madagascar, for example, has seen extinction of grazing megafauna and dramatic expansion of natural grassland at the expense of woody vegetation since human arrival (Burney et al. 2003; Kull 2012). Natural and anthropogenic factors are supported for the island's ecological transformations over the last two millennia (Crowley 2010; Virah-Sawmy et al. 2010). Human introductions have been substantial; a recent study inventoried 546 introduced species that have been naturalised, as well as 611 other introduced species that exist only under cultivation (Kull et al. 2012). These introductions almost certainly began as soon as humans arrived, though few have yet been documented in the archaeological record (Boivin et al. 2013). Other islands off the east African coast have received much less study, though translocations of a range of species are attested, including various species of shrews, rodents, mongooses, primates and domesticated plants and animals, as well as Indian civets, and Asian rats and mice (Walsh 2007; Cheke 2010; Boivin et al. 2013). About half of the terrestrial mammal species of Pemba island are known or presumed to have been introduced by humans, including all of the four-legged mammals of the island (Walsh 2007). Similarly, all four-legged mammals on each of the four Comoros Islands are human introductions (Walsh 2007). Similar processes unfolded in island Southeast Asia. Throughout the Holocene, in addition to domesticates, humans moved around various species of deer, primate, civet, cuscus, wallaby, cassowary, bird, shrew, rat and lizard to create habitats favourable to human settlement and subsistence; at least 58 wild terrestrial vertebrates alone have been anthropogenically translocated from the Indo-Malayan region to the Circum New Guinea archipelago (Heinsohn 2003).

An unambiguous picture is emerging of extensive reshaping of species distributions on islands as a global phenomenon since first human occupation. This is visible wherever archaeological and palaeoecological studies have been carried out, and new methods are providing novel insights into both chronologies and processes, as well as relationships to climatic changes.

Urbanisation and the elaboration of networks

Agriculture and the production of food surpluses paved the way for the emergence of increasingly dense, urbanised settlements, and progressively more complex and intensive networks of trade, travel and migration in the Late Holocene. Significant anthropogenic impacts in the last 4000 years are documented for a range of different societies globally. Recent studies highlight, for example, the impact that the Maya, the Egyptians, and the Romans had on their environments (give refs). Increased population size, urbanisation and agricultural expansion were key to these transformations, which had a major impact on species compositions, distributions and extinctions. The growing connectivity of societies also enabled the unprecedented anthropogenic translocation of plants and animals, as a result of both intentional and unintentional processes. Some of the species that moved would today be classed as 'invasive species', others were infectious diseases that could also move rapidly along routes of travel and trade. The dispersal of both was undoubtedly, like today, facilitated by anthropogenic habitat modification (refs).

As one of the earliest regions to undergo the transition to farming and subsequent urbanisation, the Near East was also one of the first to see significant population growth and associated impacts to biodiversity (Kaplan et al. 2009). Recent studies confirm that human impacts on regional vegetation and landscape stability were apparent across the region from Bronze Age times (Dusar et al. 2011; Roberts et al. 2011). A key driver of change in this period was the 'secondary products revolution' (Sherratt 1980, 1983), which involved the adoption of animal traction and the production of animal-derived commodities like wool and milk, as well as the intensive cultivation of orchard crops that generated marketable secondary products like olive oil, wine and dried fruits (Fall et al. 2002). Bronze Age agricultural intensification to serve growing populations and emerging markets led to significantly expanded ecological impacts in the Near East, including renewed and larger-scale forest clearance and the creation of anthropogenic forest. Pollen and archaeobotanical datasets across the region reveal pervasive turnover from deciduous to evergreen oak, and replacement of indigenous forest with cultivated orchard crops like olive (*Olea europea*), grape (*Vitis vinifera*) and fig (*Ficus carica*) (e.g., Yasuda 2000; Fall et al. 2002, Schwab et al. 2004; Neumann et al. 2007; Dusar et al. 2011). Cereal crops and vegetation indicative of anthropogenic disturbance like *Rumex*, *Plantago* and *Artemisia* also increased. Pastoralism. Transformations were not unilinear, but closely tracked changes in urbanisation and political authority, with periods of collapse and abandonment sometimes encouraging afforestation (Neumann et al. 2007), and sometimes favouring pastoralism and its associated ecological impacts (Fall et al. 2002). By 300 BC, one recent model suggests that areas suited to agriculture in Greece, Algeria and Tunisia were up to 90% under cultivation (Kaplan et al. 2009).

The emergence of socially-stratified urban societies in the Near East also appears to have been linked to the extirpation of a number of wild animal species. Recent zooarchaeological studies as well as new chronologies for desert kite activity

suggest that use of the kites, extensive stone structures thought to have been used to trap and harvest wild ungulates and perhaps other species, was particularly active between 4000-1000 BC (Tsahar et al. 2009; Bar-Oz et al. 2011; Zeder et al. 2013). Ungulate mass kills appear to have been practiced with considerable intensity across the entire Levant, perhaps for social and ritual as much as economic reasons (Bar-Oz et al. 2011; Zeder et al. 2013). The onager (*Equus hemionus*), Persian gazelle (*Gazella subgutturosa*), hartebeest (*Alcelaphus buselaphus*), Arabian oryx (*Oryx leucoryx*), and ostrich (*Struthio camelus*), all thought to have been hunted using kites, were extirpated from the southern Levant by the second millennium BC (Tsahar et al. 2009; Bar-Oz et al. 2011). Extirpations of wild taxa are also seen during this period in Egypt, linked to diverse anthropogenic impacts, such as direct hunting and habitat destruction, together with increasing aridity (Yeakel et al. 2015). A total of 37 large-bodied mammalian species are documented in Late Pleistocene/early Holocene Egypt, whereas only 8 remain today (Yeakel et al. 2015). Major extinction waves broadly coincide in Egypt and the Levant, and human activities appear to have particularly impacted large-bodied herbivores, while opportunistic ungulates and carnivores, many of which benefit indirectly from human impact (gazelle, for example, can subsist in open agricultural areas, while carnivores are attracted to human refuse), appear to have been more resilient (Bar-Oz et al. 2015). Defaunation, together with pastoral grazing, can be expected to have particularly impacted ecologically fragile arid zones, perhaps encouraging desertification and erosion (Cremaschi 2014).

Anthropogenic shaping of species abundance and diversity further intensified in the Eastern Mediterranean and Near East in the Classical era. The Roman period generally saw further expansion and intensification of agriculture. This supported both market and taxation demands, and sometimes, as in Central Anatolia, led to reshaping of species composition and abundance through overgrazing and monocropping (e.g., of *Triticum aestivum* (bread wheat) (Marston & Miller 2014). Sedimentary records across the eastern Mediterranean record the highest Holocene period rates of soil erosion and sedimentation in the Roman period (Dusar et al. 2011); these were triggered in large part by a variety of land use changes, including cultivation of previously unexploited hillslopes. Pollen diagrams similarly reveal leaps in agro-industrial crop species and indicators of disturbed, open and over-grazed landscapes in the Roman era (e.g., Fall et al. 2002; Neumann et al. 2007).

Similarly in Europe, a range of new studies demonstrate that the Roman period saw a significant expansion of agriculture, and shifts in biodiversity that had enduring effects. Agriculture intensification was linked particularly to the expansion of cultivation into previously marginal areas (through clearing, draining and irrigation), an emphasis on high yield agro-pastoralism and the growth of the cash crop industry (van der Leeuw et al. 2005, Butzer 2005; other refs). But even before the Roman period, by 300 BC, central and western European regions were, according to one recent model, between 10% and 60% deforested, and by 300 AD this had increased up to 90% in some areas (Kaplan et al. 2009).

Recent research in France suggests that Roman agriculture had an enduring effect on biodiversity, a legacy that is felt to the present day. Scientists studying large ancient forests in different regions of northern and central France have revealed dense networks of Roman buildings and settlements, and demonstrated a strong correlation between Roman sites and present-day forest plant diversity (Dupouey et al. 2002; Dambrine et al. 2007; Plue et al. 2008, 2009). The studies find that plant species richness strongly increases toward the centre of settlements, paralleling an increase in soil pH, available P and $\delta^{15}\text{N}$, and indicating long-term impact of former agricultural practices on forest biogeochemical cycles (Dupouey et al. 2001; Dambrine et al. 2007). Areas altered by Roman agriculture and settlement also favour nitrogen-demanding and ruderal species, and plants that may have been introduced as medicinal or food plants, whereas ancient woodland species like *Convallaria maialis* and the orchid *Epipactis helleborine*, which have low colonizing ability, lack suitable microhabitats and/or have a competitive disadvantage with ruderal species, were found only in areas remote from former Roman settlements (Dupouey et al. 2001).

In North Africa, a variety of processes are now understood to have altered species distributions during the Roman period. The Roman trade in wild and exotic animals, for example, fuelled by the need to stock sacred groves and hunting enclosures, to support religious ceremonies, and to supply animals – sometimes in the thousands – for entertainment and slaughter, led to local reductions in biodiversity and even extirpations in source areas like North Africa (Hughes 2003). Roman and Garamantian irrigation and agriculture, coupled with the introduction of crops from other parts of Africa, the Near East, Mediterranean, Central Asia and beyond, radically transformed desert environments and species distributions (Van der Veen et al. 1996; Barker 2002; Pelling 2005).

The transport of species – domesticated, wild and commensal – throughout the Roman empire and beyond was greatly facilitated by an expanding infrastructure of roads, harbours and canals. But species translocations into and around Europe had begun to increase already by the early part of the Classical era, with Hellenistic period introductions including a range of exotic birds (South Asian parakeet, peafowl, peacock and crow), as well as domestic chicken (refs). The domesticated cat was introduced to Greece by the 5th century BC; among its descendants are the probably the wild cats that currently inhabit Corsica and Sardinia (Gippoliti & Amori 2006; Vigne 1992). The invasive house mouse (*Mus musculus*) spread across the Mediterranean and southern Europe in the first millennium BC (Cucchi et al. 2005), and the black rat was introduced to the region by the end of the millennium (Ruffino & Vidal 2010). **One sentence on impacts.** The Roman period saw these already introduced invasive and domesticated species spread further. Most Roman rat remains in Roman Europe are within ten kilometres of the coast, suggesting maritime routes of dispersal. Sea routes were also key to the transport of livestock (Morley 2007) and many new breeds of sheep, goat, cattle, asses, horses and mules were introduced to Europe under the Romans.

The Roman era also saw the widespread translocation of the European fallow deer (*Dama dama*) and the Red deer (*Cervus elaphus*), and various species of fish, oysters and snails were intentionally translocated into Europe (Hughes 2003; Lever 2010; Parker 2008). An extraordinary array of small mammals have been moved around the Mediterranean region, including various shrews, squirrels, rabbits and dormice, as well as the genet (*Genetta genetta*), the Egyptian Mongoose (*Herpestes ichneumon*), the Algerian Hedgehog (*Atelerix algirus*) and the Barbary Ape (*Macaca sylvanus*) (Dobson 1998; Barome et al. 2001; Masseti 2005; Gippoliti & Amori 2006), and many of these translocations probably date to the Classical era. These biological exchanges have played a significant role in shaping patterns of biodiversity in the Mediterranean basin, particularly on islands, where human activities have led to the extinction of the entire autochthonous mammalian fauna and the gradual introduction of more than 25 taxa of mammals (Blondel 2008).

Plant species also moved. A recent estimate from Britain, where some of the most systematic archaeobotanical studies have been carried out, indicates that at least 50 new plant foods (mostly fruits, herbs and vegetables) were introduced to the islands in the Roman period, with many entering into cultivation (van der Veen et al. 2008, Livarda; Witcher 2013). These introductions were linked to the emergence of cash cropping and, with the arrival of plum, cherry, apple, pear and walnut trees (ultimately deriving from regions east of Europe, like central and southern Asia), the development of orchards (van der Veen et al. 2008). Genetic research suggests that the rapid spread of Dutch elm disease in the 1970s may have been facilitated by the preponderance of a susceptible variety of elm (*Ulmus procera*), a single clone of which is argued to have been widely translocated by the Romans, through the Iberian peninsula and into Britain, where it formed the core of the English elm population (Gil et al. 2004; but see Witcher 2013). Plant pathogens and pests also appear to have spread in the Roman period. Study of insect remains from British archaeological sites, for example, demonstrates the presence of a range of non-native but now established synanthropic beetle grain pests (e.g., *Sitophilus granarius*, *Oryzaephilus surinamensis* and *Laemophloeus ferrugineus*) that first appear, often in large numbers, in the Roman period, and that were probably introduced with grain imports (Smith & Kenward 2011; King et al. 2014). Many of these species are now globally disseminated (King et al. 2014).

The spread of human pathogens was similarly facilitated by intensified trade. Recent genetic evidence confirms the arrival of *Yersinia pestis*, the bacterium responsible for bubonic plague, to Europe in the late Roman period. The pathogen's East Asian origins have also been confirmed by genetic analyses; a recent study suggests that strains of *Y. pestis* may correspond with established trade routes across central Asia (Cui et al.). *Y. pestis* moved repeatedly out of East Asia through history, arriving again in the Medieval period, for example. Its devastating impact on human populations, with some 40% mortality in Europe, is reflected in patterns of forest regrowth... – black death reversed deforestation trends (e.g., Kaplan).

The anthropogenic shaping of species distributions, while more systematically studied in regions like the Near East and Europe, and for particular periods like the Roman era, appears to have similarly intensified under processes of ancient urbanisation and trade elsewhere in historical time and space. While archaeological research is more limited, human impacts to a range of biological species appear to have further intensified in the Medieval period, for example, both in Europe and beyond. Large-scale deforestation attended Medieval urbanisation in Europe, slowed only by the demographic and economic impacts of the arrival of the Black Death (Kaplan et al. 2009; Sapart et al. 2011). Medieval urban expansion dramatically reshaped species distributions and compositions in a variety of ways. Evidence is emerging for freshwater and marine ecosystem impacts in this period, and isotope data demonstrates that cities like London exceeded the capacity of regional fish supplies by the 13-14th centuries, with demand met by increasingly long distance transport of fish (Barrett et al. 2011).

The Medieval period in the Indian Ocean witnessed increased biological exchange, encouraged by expanding maritime trade and an intensification and diversification of agriculture in the Arab world (Boivin et al. 2014). Species like the black rat, house mouse, and domesticated cat and chicken all arrived in East Africa from Indian Ocean sources in the latter half of the first millennium AD (Boivin et al. refs). A highly diverse array of exotic plant species from all over the Old World, some traded in from several thousand kilometres, and others locally grown, have been identified at medieval Qara Qorum (Rösch et al 2005), and human landuse is thought to have contributed significantly to the present spatial pattern of vegetation types in Mongolia more broadly (Rösch et al 2005; Miede et al. 2007; Schlütz et al. 2008). As noted, vegetation across central and eastern Asia is increasingly seen as at least partly anthropogenic, and pastoral impacts are suggested to have significantly increased in the past thousand years (e.g., Miede et al. 2008, Kaiser et al. 2009b).

Complex civilisations in the Americas similarly shaped biodiversity and species distributions. Few sentences on Maya. The Amazon, once thought to constitute pristine rainforest, is now recognised to have been occupied by complex societies prior to European arrival. Sentence on their reshaping of rainforest. East Asia and rice agriculture, methane.

Broad patterns

We outline the general patterns that emerge from our review:

1. Through time we see evidence for broadly increasing rates of species translocation, extinction and biodiversity reshaping. This acceleration is not constant, but rather characterised by pulses and pauses that reflect local, regional, and sub-global cultural and biological transformations.
 - a. Anthropogenic species translocations go back at least to the late Pleistocene, and long-distance translocations began in the Neolithic, accelerating in the Bronze Age and later. These translocations, while less frequent in earlier than later periods, can nonetheless not be dismissed as rare and of little consequence. Many, for example the

arrival of Near Eastern herbivores in the highlands of Tibet, would have significant consequences and cascade effects. The Columbian Exchange must be placed in broader prehistoric and historical context.

2. Ancient and modern human activity has impacted the relative abundance, distribution patterns, extinction rates, and translocation pathways of species globally. There is a strong link between present-day patterns of biodiversity and historical processes.
3. This is niche construction.
4. The combined effects of human activity over the millennia include the creation of radically transformed and/or highly cosmopolitan species assemblages on all landmasses. 'Pristine' landscapes do not exist, and in, in many cases, have not existed for millennia.

My impression, partly based on my own experience and partly based on conversations with colleagues, is that the common default assumption among geomorphologists is that a landscape that does not have obvious, contemporary human alterations has experienced lesser rather than greater human manipulation. Based on the types of syntheses summarized earlier, and my experience in seemingly natural landscapes with low contemporary population density but persistent historical human impacts (e.g., [Wohl, 2001](#)), I argue that it is more appropriate to start with the default assumption that any particular landscape has had greater rather than lesser human manipulation through time, and that this history of manipulation continues to influence landscapes and ecosystems. To borrow a phrase from one of my favorite paper titles, we should by default assume that we are dealing with the ghosts of land use past ([Harding et al., 1998](#)). This assumption applies even to landscapes with very low population density and/or limited duration of human occupation or resource use (e.g., [Young et al., 1994](#), [Wohl, 2006](#), [Wohl and Merriitts, 2007](#) and [Comiti, 2012](#)). (Wohl 2013 Wilderness is dead)

Vs. Grayson 2001 – who emphasizes how archaeologists naturally acquire a recognition of human manipulation of environments. He points out that environments encountered by Europeans as they expanded across the globe were to one degree or another anthropogenic (3).

Discuss Amazon here as a case of non-pristine landscape whose biodiversity has been heavily shaped by humans.

5. Despite a tendency to polarise discussions of historical human impacts, we see evidence for a range of historical scenarios from the catastrophic to the sustainable.
 - a. Impact (of extinction) depends on how significantly a species interacts with other species in the community (predator, competitor, symbiont, mutualist, prey); loss may result in little or no adjustment, at other end are species that interact significantly in communities with strongly linked food webs (Estes et al 1989)
 - b. Resilience: Butzer, K. W., & Harris, S. E. (2007). Geoarchaeological approaches to the environmental history of Cyprus: explication and critical evaluation. *Journal of Archaeological Science*, 34(11), 1932-1952.
 - c. Resilience and sustainability in the Med - Blondel would see translocations plus the hybridisation and proliferation of breeds as an increase in biodiversity.
 - d. Kareiva, P., Watts, S., McDonald, R., & Boucher, T. (2007). Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, 316(5833), 1866-1869.
 - e. **Global Change and the Ecology of Cities** Nancy B. Grimm^{1,*}, Stanley H. Faeth¹, Nancy E. Golubiewski², Charles L. Redman³, Jianguo Wu^{1,3}, Xuemei Bai⁴, John M. Briggs¹

Implications

Genetic, archaeological and palaeoecological studies are showing us a world that has been much more biologically fluid than once believed. We review and critically assess the following implications of this:

1. The start of the Anthropocene – the period of human domination of Earth's systems – is much earlier than conventionally understood.
 - a. Contra Steffen et al 2007 (and 2011) – see Braje & Erlandson 2013 – preindustrial societies did not have a negligible impact. Effects not local and transitory.
2. Historical, human-mediated changes to biodiversity can help scientists to better understand contemporary human-ecology interactions and predictively model future ones. They can inform, for example, strategies of invasive species management, pandemic risk assessment and ecological conservation.
 - a. Determining the consequences of past ecological disturbance will inform predictions of how modern communities may respond to ongoing anthropogenic or climatic factors (Yeakel et al. 2015)
 - b. Long-term impacts of human activities on species abundance, distribution, etc can be examined through the long-term record offered by archaeology.
 - c. Can't understand present day landscape processes without recognising past processes that have shaped and continue to shape landscapes – see, e.g., Lindborg, R., & Eriksson, O. (2004). Historical landscape connectivity affects present plant species diversity. *Ecology*, 85(7), 1840-1845.
 - d. However, there is a need for greater exploration of the implications of palaeoecological and archaeological findings, and the application of historical inferences to present day issues and challenges. We cannot just sit around and wait for researchers from other fields or policy makers to come to us.
3. However, conservation approaches that seek a return to original ecological conditions might be better off adopting approaches that privilege pragmatic solutions over ideal ones.
 - a. Rewilding – Donlan et al 2005; Wolverson 2010 – see Braje & Erlandson 2013; see Reversing defaunation: Restoring species in a changing world (Seddon et al 2014)
 - b. Pedrono, M., Griffiths, O. L., Clausen, A., Smith, L. L., Griffiths, C. J., Wilmé, L., & Burney, D. A. (2013). Using a surviving lineage of Madagascar's vanished megafauna for ecological restoration. *Biological Conservation*, 159, 501-506.
4. Historical anthropogenic processes have at times had catastrophic ecological impacts, but at other times have played a significant role in generating sustainable ecosystems optimally suited to addressing human subsistence and health needs as well as demographic pressures. The legacy of both impacts is felt today.
 - a. Blondel 2006

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